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IDEA AND PERSPECTIVE

The effects of intransitive competition on coexistence

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Abstract

Coexistence theory has been developed with an almost exclusive focus on interactions between two species, often ignoring more complex and indirect interactions, such as intransitive loops, that can emerge in competition networks. In fact, intransitive competition has typically been studied in isolation from other pairwise stabilising processes, and thus little is known about how intransitivity interacts with more traditional drivers of species coexistence such as niche partitioning. To integrate intransitivity into traditional coexistence theory, we developed a metric of growth rate when rare, $\overline{\Delta r_i}$, to identify and quantify the impact of intransitive competition against a backdrop of pairwise stabilising niche differences. Using this index with simulations of community dynamics, we demonstrate that intransitive loops can both stabilise or destabilise species coexistence, but the strength and importance of intransitive interactions are significantly affected by the length and the topology of these loops. We conclude by showing how $\overline{\Delta r_i}$ can be used to evaluate effects of intransitivity in empirical studies. Our results emphasise the need to integrate complex mechanisms emerging from diverse interactions into our understanding of species coexistence.

Keywords

Competition network, indirect interactions, intransitive loop, invasion growth rate, niche theory, rock-paper-scissor, stabilising mechanism.

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INTRODUCTION

Understanding coexistence in species-rich ecosystems is an important and long-held aim of community ecology (e.g. Gause 1934; Diamond 1975; Tilman 1982). Recent advances in theory (Chesson 2000) coupled with field observations, experiments, and modelling have given ecologists the tools to quantify specific coexistence mechanisms (Angert *et al*. 2009), the contribution of niche and fitness differences to community dynamics (Levine & HilleRisLambers 2009; Chu & Adler 2015), and the link between functional traits and coexistence (Kraft *et al*. 2015). However, all of these theoretical and empirical approaches focus on pairwise species interactions, ignoring the more complex chains of indirect interactions that can emerge in diverse natural communities.

Recent studies of intransitive competition have reinvigorated interest in the complex interactions possible in competition networks (Laird & Schamp 2015; Soliveres *et al*. 2015). This ecological analogue to the rock-paper-scissor game (see Box 1) may in fact promote biodiversity in a large variety of plant and animal systems (Buss & Jackson 1979; Armas & Pugnaire 2011; Soliveres *et al*. 2015). In theory, intransitivity can allow more species to coexist than there are limiting resources (Huisman *et al*. 2001; Allesina & Levine 2011) and may occur when several resources limit population growth but no one competitor is best at competing for all resources (e.g. Lankau & Strauss 2007; Allesina & Levine 2011; Armas & Pugnaire 2011; for a review see Gallien 2017). Prior mathematical work has shown that intransitive loops containing an odd number of species can stabilise species coexistence, whereas loops containing an even number of species have destabilising effects on species abundances (see Box 1; Allesina & Levine 2011; Vandermeer 2011).

Despite these theoretical advances, intransitive competition is not well integrated into our more general understanding of how coexistence emerges between pairs of competitors. This situation arises partly because most of the literature on intransitive competition has developed independently of recent pairwise coexistence theory. Theoretical studies of intransitivity have tended to focus on the most simple three species case (Kerr *et al*. 2002; Reichenbach *et al*. 2007; Schreiber & Killingback 2013; but see Laird & Schamp 2015), which is often of limited relevance to natural communities. In contrast, empirical studies of intransitivity in species-rich natural communities have developed techniques for inferring interaction networks from observational co-occurrence data or transition-based models, but do not quantify the effect of intransitivity on species coexistence (e.g. Buss & Jackson 1979; Quinn 1982; Ulrich *et al*. 2014; Soliveres *et al*. 2015; but see Wootton 2001). Integrating findings related to intransitive competition into our traditional framework for pairwise species coexistence would make our understanding of coexistence more complete.

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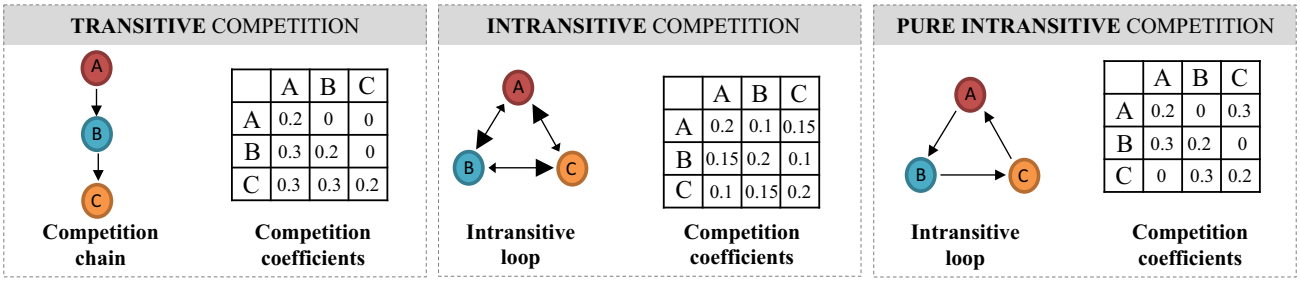
Box 1 General description of intransitive competition

In a three species system {A, B, C}, *transitive interactions* occur if species A is a better competitor than species B (which we denote A>B), species B is better than species C (B>C), and A is a better competitor than species C (A>B>C and A>C). *Intransitive interactions* occur if A>B, B>C, and C is a better competitor than A. The resulting *intransitive loop* of competitive interactions, A>B>C>A, is the familiar 'rock-paper-scissor' game (Gilpin 1975; May & Leonard 1975). Intransitivity can occur either in combination with stabilising niche difference mechanisms, or in the absence of stabilising mechanisms (as usually assumed when using game theory payoff matrices; here called *pure* intransitivity; Figure B1).

Figure B1 Representations of transitive, intransitive and *pure* intransitive competitive interactions in a tree species system (A, B, C). Competition can be presented in a competitive network fashion (where arrows point to the weaker competitor), or with competition matrices (showing all pairwise competition coefficients).



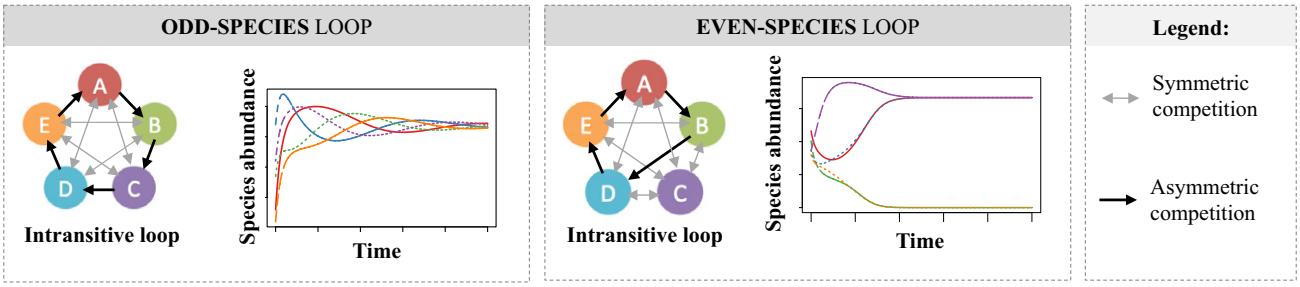
	A	B	C
A	0.2	0	0
B	0.3	0.2	0
C	0.3	0.3	0.2

	A	B	C
A	0.2	0.1	0.15
B	0.15	0.2	0.1
C	0.1	0.15	0.2

	A	B	C
A	0.2	0	0.3
B	0.3	0.2	0
C	0	0.3	0.2

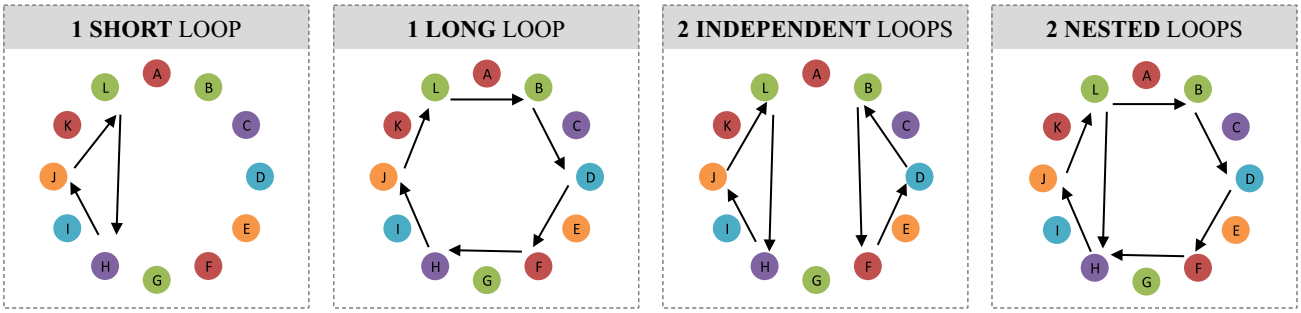
In species-rich communities, intransitive loops can contain various numbers of species, and their impact on species coexistence depends on their length. An odd-length loop (e.g. containing 3, 5, 7… species) has a stabilising effect on species coexistence, while an even-length loop (e.g. containing 4, 6, 8… species) has a destabilising effect on species abundances as half of species will increase their abundances at the cost of the other half of the species (Figure B2; Durrett & Levin 1998; Allesina & Levine 2011). In cases where species fitness differences are greater than their stabilising niche differences (e.g. under pure intransitive interactions) the abundance of destabilised species tends towards zero.

Figure B2 Species abundance dynamics for a 5-species community containing an intransitive loop of either an odd or an even number of species. The species are indicated by distinct letters and colours, and arrows indicate weak competitors.



In species-rich communities it is also possible that more than one intransitive loop is present. If so, these loops can be independent or nested within each other: two independent loops involve two different sets of species, while two nested loops are composed of two sets of species nested within each other (Figure B3).

Figure B3 Illustration of 13-species communities containing one short or one long intransitive loop (1st and 2nd panels), and communities containing two independent or nested intransitive loops (3rd and 4th panels).



One primary obstacle prevents such integration: each tradition relies on distinct analytical approaches and models. Theoretical studies of intransitivity involving many species typically use a game theory 'payoff matrix' which describes, for each pair of competitors, which species wins or loses in competition (Box 1; Leyton-Brown & Shoham 2008). As a consequence, they examine scenarios in which coexistence is impossible in the absence of the intransitive network, which we refer to as 'pure' intransitivity. This approach ignores pairwise competitive processes that might otherwise stabilise coexistence. In contrast, much coexistence research, in the tradition of the Lotka-Volterra models, focuses on the *community matrix*, which specifies each species' quantitative per capita intra- and interspecific effects (Case 2000).

'Pure' intransitivity is unlikely to occur in nature because 'rock-paper-scissor' communities could not easily assemble: if only two of the three species are present, one will be excluded before the third can arrive. Only in the unlikely case where all three species were simultaneously introduced would coexistence be possible. However, this does not mean that intransitive competition plays no role in maintaining diversity. If species pairs possess stabilising niche differences, and can therefore coexist without intransitivity, the intransitivity might further stabilise coexistence or enable the persistence of additional species. Intransitivity in natural communities is thus more likely to be 'partial' than 'pure'.

Recognising the potential for partial intransitivity raises a number of new questions. How does the length of intransitive loops affect the strength and importance of intransitivity against a backdrop of pairwise stabilising mechanisms? Additionally, when pairwise coexistence mechanisms operate simultaneously with intransitive competition, all coexisting species need not be part of the intransitive loop. In this case, how does the number and configuration of intransitive loops in a system, including their nestedness (Box 1), influence the coexistence of species inside and outside the intransitive loop?

Here, we explore the effects of intransitive competition on coexistence in the presence of pairwise stabilising mechanisms. This approach enables us to explore the impacts of intransitivity using the same methods traditionally used to study pairwise coexistence mechanisms. Specifically, we develop a metric based on invasion growth rates, $\overline{\Delta r_i}$, that shows how coexistence is enhanced or reduced by intransitive competition. We apply this metric to Lotka-Volterra simulations that include intransitive competitive interactions of various strengths, to quantify the importance of this phenomenon in communities of increasing complexity. We first use a simple three-species competition model to demonstrate that $\overline{\Delta r_i}$ can be used to quantify the influence of intransitivity on species coexistence. We then employ $\overline{\Delta r_i}$ to describe the importance of intransitive interactions in more complex, species-rich systems. Here, species loops are set up to vary in length, number, and nestedness, with particular attention to the influence of the intransitive loop on the coexistence of species in the loop, as well as those outside of it. These simulations also illustrate how our metric could be applied to empirically parameterised models of competitive dynamics and experiments in model systems.

METHODS

The invasion growth rate in a three-species Lotka-Volterra model

In a Lotka-Volterra competition model, the growth rate of species i can be expressed as:

$$\frac{dN_i}{dt} = \lambda_i N_i\left(1 - \alpha_{ii}N_i - \sum\nolimits_{j\neq i}\alpha_{ij}N_j\right) \quad (1)$$

where λ_i is the intrinsic rate of growth of species i, N_i and N_j are the abundances of species i and species j respectively, α_{ii} is the intraspecific competition coefficient, while α_{ij} is the interspecific competition coefficient describing the per capita effect of species j on species i.

The invasion growth rate, r, is the per capita rate of increase in a focal species' abundance when it is rare and the other species of the community, the residents, are at equilibrium. If under such conditions $\frac{dN_i}{dt}\cdot\frac{1}{N_i} > 0$ for all species i, coexistence is stable in a two-species system and possibly stable in a system with three or more competitors. For a three-species system {A, B, C}, invasion growth rates can be calculated analytically (see Appendix S1): the growth of species A when species B is the only resident (i.e. when C is absent) is:

$$r_{A,-C} = 1 - \frac{\alpha_{AB}}{\alpha_{BB}} \quad (2)$$

and the invasion growth rate of species A when species B and C are resident (and coexist) is:

$$r_A = 1 - \frac{\alpha_{AB}\alpha_{CC} - \alpha_{AB}\alpha_{BC} + \alpha_{AC}\alpha_{BB} - \alpha_{AC}\alpha_{CB}}{\alpha_{BB}\alpha_{CC} - \alpha_{BC}\alpha_{CB}} \quad (3)$$

We used this model to study the coexistence of three species in communities with varying degrees of intransitivity (i.e. where species pairwise coexistence ranges from possible to impossible; see Box 1). All three competitors are involved in the intransitive loop via a specific arrangement of fitness differences (A>B>C>A), but each pair of species is also stabilised by pairwise niche differences. The influence of intransitivity on invasion growth rates in these simulated communities was evaluated across a large range of intransitive competition matrices, varying in their strengths of fitness differences (1000 different matrices). The matrices ranged from purely symmetric matrices (all $\alpha_{ii} = 0.002$ and all $\alpha_{ij} = \alpha_{ji} = 0.001$) to intransitive matrices with gradually increasing pairwise fitness differences (i.e. competitive differences) between species. Prior analysis of the two-species version of this model has shown that pairwise competitive dominance is determined by the average fitness difference $\sqrt{\frac{\alpha_{ii}\alpha_{ij}}{\alpha_{jj}\alpha_{ji}}}$, and coexistence is stabilised as niche overlap $\sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{jj}\alpha_{ii}}}$ approaches zero (the stabilising niche difference = 1 – niche overlap; Chesson 2012). Thus, to incorporate three-way intransitive competition, the interaction coefficients determining the pairwise fitness differences were arranged in an intransitive fashion, where $(\alpha_{BA} = \alpha_{CB} = \alpha_{AC}) > (\alpha_{AB} = \alpha_{CB} = \alpha_{CA})$, and species A>B>C>A.

We explored the effects of increasingly strong intransitive competition by modifying the interspecific interaction coefficients to increase the average fitness difference in each pairwise interaction. We did so in a way that did not change the

pairwise niche overlap, which we always set to 0.5. To this end the matrix of competition coefficients is defined as:

$$\begin{bmatrix} \alpha_{AA} & \alpha_{AB} & \alpha_{AC} \\ \alpha_{BA} & \alpha_{BB} & \alpha_{BC} \\ \alpha_{CA} & \alpha_{CB} & \alpha_{CC} \end{bmatrix} = 0.001 \cdot \begin{bmatrix} 2\sqrt{\theta} & \theta & 1 \\ 1 & 2\sqrt{\theta} & \theta \\ \theta & 1 & 2\sqrt{\theta} \end{bmatrix} \quad (4)$$

where decreasing θ increases the pairwise fitness differences while keeping the pairwise niche overlaps constant. Fitness differences ranged from a minimum of 1 (θ = 1 and the competition matrix is $\begin{bmatrix} 0.002 & 0.001 & 0.001 \\ 0.001 & 0.002 & 0.001 \\ 0.001 & 0.001 & 0.002 \end{bmatrix}$) to a maximum of 3 (θ = 0.111 and the competition matrix is $\begin{bmatrix} 0.000666 & 0.000111 & 0.001000 \\ 0.001000 & 0.000666 & 0.000111 \\ 0.000111 & 0.001000 & 0.000666 \end{bmatrix}$). A fitness difference of two perfectly counterbalances the stabilising forces (given that niche overlap in the matrix = 0.5), and thus defines the boundary between stable pairwise coexistence and exclusion. Therefore, when fitness differences > 2, competitive exclusion occurs for isolated species pairs, but might not occur if species benefit from intransitivity when embedded in the full community. The values for niche and fitness differences were chosen to match typical empirical measures of niche and fitness differences found in nature (e.g. niche differences ranging from 0.5 to 1, and fitness differences from 1 to 3, as in Chu & Adler 2015). Finally, we note that our use of fitness differences here applies specifically to the pair of competitors, such that pairwise competitive fitness depends on the identity of one's competitor (as in Godoy *et al.* 2017).

To evaluate how intransitivity stabilises coexistence in these three-species systems, we estimated the growth rates of each of the three species invading a system with either one or both of the other competitors at equilibrium. In the absence of any intransitivity, the elimination of one resident will *increase* the focal species' invasion growth rate as long as niche overlap > 0. This occurs because the removal of one resident species means less competition for the invader. In contrast, when intransitivity is present, the removal of a resident can break the intransitivity and *decrease* the focal species' invasion growth rates. The extent to which greater pairwise fitness differences increase invasion growth rates in the presence of both competitors therefore indicates the importance of the intransitivity to coexistence. For this analysis, we used competition coefficients that produce homogeneous pairwise fitness differences: A has the same advantage over C that C has over B and B has over A. To test the sensitivity of our results to the variation in the matrix of coefficients, we repeated the analysis with four alternative scenarios of heterogeneous fitness differences: (1) where one species pair had a relatively small fitness difference (i.e. A > > B > > C>A), (2) where two species pairs had relatively small fitness differences (i.e. A > > B > C>A), (3) where all species pairs had different values of fitness differences (i.e. A > > > B > > C>A), (4) where intransitive interactions were reversed into transitive ones (i.e. A>B>C and A>C; see details in Appendix S2).

While coexistence can also be studied by analysing the stability of the equilibrium solutions to the model (Novak *et al.* 2016), our metric based on invasion growth rates has multiple advantages: (1) it integrates intransitive competition into modern coexistence theory, which focuses on invasion growth rates, (2) it is straightforward to understand and thus accessible to a wide audience of researchers, and (3) it does not require estimating the matrix of competition coefficients; the metric can be directly quantified from experiments or analytically intractable multispecies population models parameterised with observational data, as described in the Discussion.

$\overline{\Delta r_i}$: A new measure of intransitivity strength and importance

To quantify the importance of intransitivity for the stability of species coexistence, we propose a new measure, $\overline{\Delta r_i}$. This index is based on the difference between the invasion growth rate of a focal species *i* when all other species of the community (the 'residents') are present and equilibrated, and the invasion growth rate of the same focal species when all residents except for one are present and equilibrated. With the first invasion growth rate, the focal species can benefit (or be harmed) by the intransitivity, while in the second, the intransitivity is broken by the removal of a species in the loop, and thus the difference of these growth rates (when averaged over the removal of each resident) provides a measure of the importance of the intransitivity for a given focal species. More formally,

$$\Delta r_i = \frac{\sum_{j \neq i}^{S} r_i - r_{i,-j}}{S-1} \quad (5)$$

where r_i is the invasion growth rate of species *i* invading the full community of resident species (as estimated with eqn 3 for a three-species community), and $r_{i,-j}$ is the invasion growth rate of species *i* invading the same community after the removal of species *j* (as estimated with eqn 2 for a three-species community). Averaging over the growth rate differences caused by the removal of each resident species *j* (with *S* species in the system), Δr_i shows the average change in the invasion growth rate of species *i* following the extinction of any one resident species. Δr_i can then be computed for each species *i* in the system, and the overall importance of intransitivity for all species can be estimated as the *mean* Δr_i $\overline{\Delta r_i}$. In our community set up, if B and C are the residents and pairwise coexistence is impossible (fitness differences > niche differences) then B outcompetes C when A is depressed to low density and r_A equals $r_{A,-C}$ ($r_A - r_{A,-C} = 0$). In a more species rich system with some competitors *outside* the intransitive loop, $\overline{\Delta r_i}$ can be calculated either including or excluding those competitors, meaning that we can estimate either the stabilising effect of intransitivity on the species within the loop, or at the general scale of the community.

Positive values of $\overline{\Delta r_i}$ indicate that intransitivity contributes to coexistence. In other words, the pairwise fitness differences present in the community are arranged in such a way that removing a resident from the community will actually hurt the invader. Conversely, negative values indicate that any positive effect of intransitivity is smaller than the traditional effects of niche overlap: removing a resident helps the invader.

The influence of partial-intransitivity on complex multi-species coexistence

We used $\overline{\Delta r_i}$ to describe the impact of intransitive loops in more complex systems containing 15 species. We specifically explored the influence of (1) loop length, (2) loop number, and (3) loop nestedness on the coexistence of those species involved in these loops and on the coexistence of all species in the communities. We evaluated the influence of intransitive loop length with simulations of communities containing only one loop, but between 3 and 15 species in the loop (13 scenarios). The influence of loop number was evaluated with simulations of communities containing from 1 to 5 intransitive loops of three species. The loops were set to be independent: no species was involved in more than one loop. To evaluate the influence of nested loops, we additionally simulated communities containing one intransitive loop including all 15 species (the outer loop), plus another nested loop including from 3 to 14 species. For each of these scenarios, we varied the strength of pairwise fitness differences between species in the intransitive loops from 1 (all $\alpha_{ij} = \alpha_{ji}$) to 3, and calculated $\overline{\Delta r_i}$ and the standard deviation around $\overline{\Delta r_i}$ (Appendix S3).

In Lotka-Volterra models of species rich communities of competitors, the invasion growth rate of species i is $\lambda_i\left(1-\sum_{j\neq i}\alpha_{ij}N_j^*\right)$, where N_j^* is the equilibrium abundance of species j. However, finding an analytical solution for the equilibrium abundances (N_j^*) can be difficult, because the system sometimes shows heteroclinic cycles. For the 15-species systems we therefore estimated species' abundances at equilibrium from simulations, using Euler's method to approximate local population growth from eqn (1) and the competition matrices, with adaptive time steps (following Stevens 2010 recommendations) and the Runge-Kutta method (Cash and Karpe parameters were as provided in the deSolve R package; Soetaert *et al*. 2010). These simulations were initialised with all species except the focal species i at initial abundances randomly drawn from a normal distribution centred on 170 (SD = 20). After a spin-up of 2000 time steps, all resident species reached equilibrium abundances, and these abundances were used to calculate the invasion growth rates and our $\overline{\Delta r_i}$ index (eqn 5).

In most of our simulated communities, species abundances tend towards a stable focal point attractor (i.e. species abundances stabilise at one value), and thus repeating the simulation experiments to estimate the invasion growth rates always gives the same results. However, in the case of the nested intransitive loop simulations with large fitness differences between species pairs, the system tends towards heteroclinic cycles (i.e. species abundances oscillate with increasing periods), and thus repeating the invasion experiment is needed to identify general trends. In these cases we repeated all invasion simulations 100 times.

We validated our simulation approach in a three-species system by comparing growth rates obtained from dynamic simulations with growth rates calculated using eqns 2 and 3; both approaches gave very similar results (see Appendix S4). All simulations were performed with the software R (R Development Core Team 2015) and the *deSolve* package (Soetaert *et al*. 2010).

RESULTS

Intransitivity increases the stability of coexistence in a three-species system

With rock-paper-scissor competition between species (A, B, and C) and imperfect niche overlap, increasing the pairwise fitness differences increased the invasion growth rate of A in the presence of both B and C (Fig. 1a). When invading only the competitively superior C, the growth rate of A declined with increasing fitness differences; the reverse effect emerged when A invaded the competitively inferior species B. When all interactions between species are symmetric such that there is no intransitivity, the growth rate of A invading a resident community containing both B and C was less than its growth rate when invading monocultures of B or C (left hand side of Fig. 1a). This result reflects niche packing in the absence of intransitivity – more species in the resident community increases the overlap in resource use between the community and the invader. In other words, in situations where the intransitive loop is unimportant, removing one resident species increases invasion growth rates. In contrast, when the intransitive loop is important (i.e. high fitness differences in Fig. 1a), then removing a resident species on average decreases invasion growth rates. Since fitness differences were homogeneous, these results are identical irrespective of whether the focal species is A, B, or C. We can therefore conclude that intransitive loops help stabilise species coexistence in this three-species systems.

We repeated this analysis to determine whether the results of the homogeneous fitness differences case hold for the alternative scenario of heterogeneous fitness differences: (1) where one species pair had a relatively small fitness difference (i.e. A > > B > > C>A), (2) where two species pairs had relatively small fitness differences (i.e. A > > B>C>A), (3) where all species pairs had different values of fitness differences (i.e. A > > > B > > C>A), (4) where intransitive interactions were reversed into transitive ones (i.e. A>B>C and A>C; Appendix S2). In each of these four scenarios we found qualitatively the same results as in the homogeneous fitness differences analysis presented above. Results also showed that increasing the heterogeneity of the fitness differences decreased the positive effect of intransitive interaction loops (see Appendix S2 for details on the results): species coexistence was more stable when species fitness differences were more homogeneous.

Measuring the importance of intransitivity with $\overline{\Delta r_i}$

The second objective of the study was to provide a tool to quantify the importance of intransitive competition to coexistence. In a three-species system (A, B, C) containing an intransitive loop (species A>B>C>A), the invasion growth rate of A increased when B was removed ($r_A - r_{A,-B} > 0$; upper dashed line in Fig. 1b). Yet the invasion growth rate

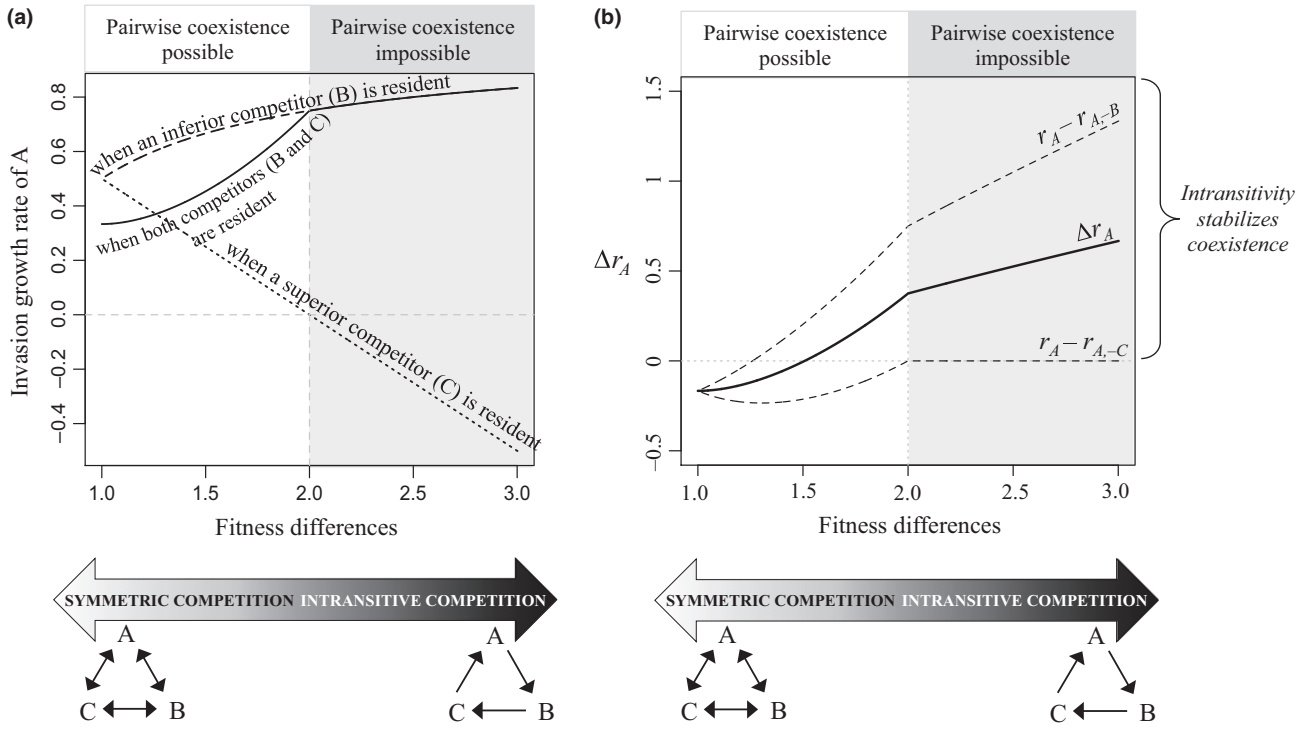


Figure 1 Influence of intransitive competition on the stability of species coexistence (a) and the illustration of our growth rate when rare metric, Δr_i, to quantify the influence of intransitive competition on coexistence (b). (a) In a three-species system {A, B, C}, the invasion growth rate of species A when B is resident ($r_{A,-C}$; dashed line), when C is resident ($r_{A,-B}$; dotted line) and when B and C are residents (r_A; solid line) vary with the strength of fitness differences. In this case, a fitness difference score of 1 makes the system perfectly symmetric (e.g. species A has the same effect on species B that B has on A), and increasing fitness differences increases the asymmetry in pairwise interactions (e.g. species A has a greater effect on B than B has on A). (b) When considering species A, Δr_A (solid line) is the average between the high values of $r_A - r_{A,-B}$ (upper dashed line; as A is a better competitor than B) and the low values of $r_A - r_{A,-C}$ (lower dashed line; as C is a better competitor than A). Δr_A's positive values indicate a stabilising effect of intransitive competition on species coexistence. Given the chosen competition matrices all of which have stabilising niche differences = 0.5, pairwise coexistence is possible with fitness differences < 2, while competitive exclusion occurs when fitness differences are > 2 [grey shaded area in (a) and (b)].

of A when C was removed (lower dashed line in Fig. 1b) depended on the strength of fitness differences: it decreased if pairwise coexistence was possible ($r_A - r_{A,-C} < 0$; left hand side of Fig. 1b), or remained constant if pairwise coexistence was impossible due to competitive exclusion of one resident ($r_A - r_{A,-C} = 0$; right hand side of Fig. 1b). This discontinuity in Δr_i occurs at a fitness difference of 2, which is the fitness difference at which B excludes C, and thus r_A becomes equal to $r_{A,-C}$. Overall, the average of these growth rate ratios, $\overline{\Delta r_i}$, shown by the solid line, increased with increasing pairwise fitness differences (which increased the strength of the intransitive competition), and became positive at a fitness difference of 1.5. Below this value, the niche packing effect of more competitors overwhelms the intransitivity; above this value, the intransitivity generates a net benefit. This general result is supported for homogeneous fitness differences between species pairs (Fig. 1b), but also under our four scenarios of heterogeneous fitness differences.

Properties of intransitive loops in complex systems

Using our measure of $\overline{\Delta r_i}$ (which averages across species in the invader state), we were able to confirm that the influence of loop length depended on whether the loop was composed of an odd or an even number of species. In the case of an odd number of species, our results showed the stabilising effect of intransitive loops, with generally positive $\overline{\Delta r_i}$ values given that some minimum fitness difference was met (yellow to red lines in Fig. 2). We further found that the importance of intransitive interactions to coexistence of species within the loop (Fig. 2a), and all species regardless of their loop membership (Fig. 2b), increased with the length of the loop (the fraction of the community contained within the loop). Similarly, with an even number of species in the intransitive loop we found increasing destabilising effects of intransitivity with loops of increasing lengths (blue lines in Fig. 2). Introducing a competitive hierarchy among the species not involved in the intransitive loop generally reduced the stabilising effects of intransitivity (see Appendix S5).

Increasing the number of independent three-species loops in a 15-species system increased the importance of intransitive interactions for the invasion growth rates of species in these loops (Fig. 3a). However, increasing the number of loops in the system (involving more species in loops) only increased the average importance of intransitivity for coexistence when at least two *three-species* loops were present (Fig. 3b).

Finally, when exploring systems with one loop nested within the full 15-species loop, the effect of increasing the length of the inner loop once again differed for odd and even length

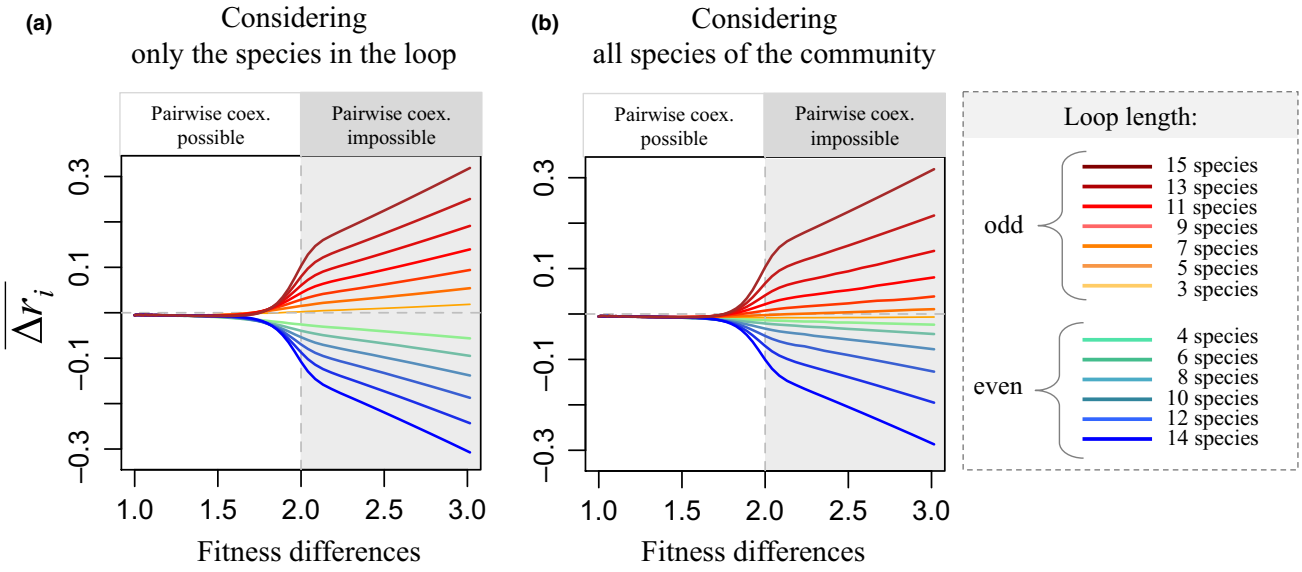


Figure 2 Importance of intransitive loop lengths in a 15-species system when considering (a) only the species involved in the intransitive loops, or (b) all species of the communities. The loop lengths are indicated by bright to dark colours, with odd-loops highlighted by reddish colours while even-loops were highlighted by bluish colours (see colour legend on the right panel). The importance of intransitive loops is measured with $\overline{\Delta r_i}$, and grey shadings indicate conditions under which species pairwise coexistence is impossible.

loops. Odd-length inner loops further stabilised species coexistence, with an increasing stabilising effect for longer inner loops (yellow to red lines in Fig. 3c and d). However, with large fitness differences between species, the influence of odd nested loops on all species of the community became more erratic and showed non-linear patterns. These non-linear patterns are explained by the fact that increased fitness differences led to the sequential extinction of residents, which switched the loop length from odd to even and back again and thus provoked an alternation of stabilising and destabilising effects. With even-length inner loops (embedded in an odd length 15-species loop), we found initially negative but eventually positive $\overline{\Delta r_i}$ scores for the species in the inner loop with intermediate fitness differences (i.e. the positive effects only occurred for fitness differences greater than 1.8, and not 1.5 as found for odd-loop lengths). This indicates that the stabilising effects of the odd outer loop were stronger than the destabilising effects of the inner loop. All stabilising effects were greater (i.e. higher $\overline{\Delta r_i}$ scores) when considering only the species in the inner loop than when considering all species in the system.

DISCUSSION

The $\overline{\Delta r_i}$ index, our metric for quantifying the importance of intransitivity in promoting species coexistence, is an important contribution for two reasons. First, it provides an intuitive measure to assess intransitive interactions in diverse communities, with positive values indicating that intransitive interactions have a stabilising effect on species coexistence that is strong enough to overcome the negative effects of niche overlap. Second, it brings intransitive interactions into the invasion growth rate framework common in modern coexistence theory, and enables the study of complex communities whose dynamics reflect pairwise niche differences as well as transitive and intransitive competitive interactions.

Our results based on the $\overline{\Delta r_i}$ metric confirm that the stabilising effects of intransitive loops mainly depend on whether they are composed of an odd or an even number of species. We also found that loop length, loop number and loop nestedness can mitigate stabilising and destabilising effects of intransitive interactions. In odd-species loops, the stabilising effects of intransitivity generally increased with increasing intransitive loop length. This result held true when considering either single or multiple independent loops. Indeed, the longer an intransitive loop, the more species are included in that loop, and the less niche packing effects imposed by other species in the community matter. These results confirm that intransitive interactions can act across large numbers of species, even in the presence of pairwise niche differences. Our results also demonstrate that increasing the number of independent loops within a community, and thus the inclusion of more species in loops, had a stabilising effect on the overall community. In odd-species loops nested within larger odd-species loops, we found that the stabilising effects became more difficult to anticipate, as these effects strongly depended on the size of the inner loops as well as the strength of fitness differences between the species, in some cases leading to non-linear trends and high uncertainty.

In even-species loops, we generally found destabilising effects of intransitive competition. If we considered intransitivity effects on all species, including those in- and outside of the loop, longer loop lengths had an increasing destabilising effect (Fig. 2b). This makes sense given that more species were included in the destabilising, even-species length, intransitive loop. Similarly, in even-species loops nested within larger odd-species loops, we found that destabilising effects tended to

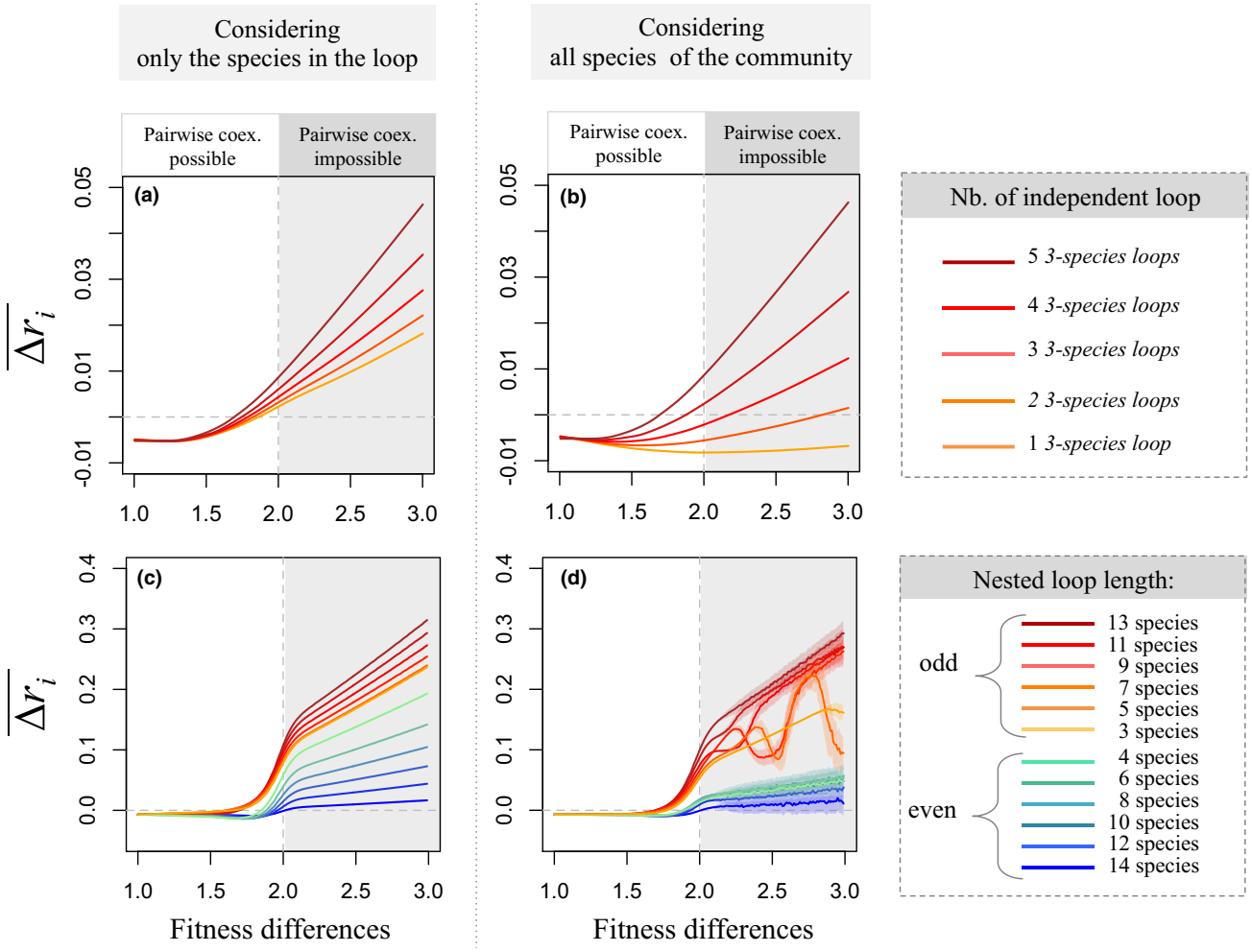


Figure 3 Importance of multiple independent (a and b) and nested (c and d) intransitive loops in a 15-species system when considering (a and c) only the species involved in the intransitive loops, or (b and d) all species of the communities. The importance of intransitive loops is estimated with $\overline{\Delta r_i}$, and varies along a gradient of pairwise species fitness differences. Each independent loop is composed of three species competing in an intransitive fashion. Nested loops are composed of one large 'outer' loop of 15 species, in which is nested a smaller 'inner' loop of 3–14 species. The solid lines on the nested loop panels (c and d) show mean trends (across 100 repetitions) and the standard deviation around these trends is represented by shaded areas (note that the standard deviation on panel c is so small that it is nearly invisible).

increase with the size of the inner loops, although for high fitness differences between species their impact on the stability of species coexistence became less predictable. Such complexities emphasise the need for caution when inferring the effects of intransitive interactions in species rich systems. Indeed, multiple intransitive loops can have opposing effects on species coexistence, and may collectively destabilise species diversity. In fact, in highly complex systems containing both transitive and intransitive interactions, the $\overline{\Delta r_i}$ index can be employed to quantify the influence of each species on the net intransitivity effect. We might expect, for example, different values for species inside and outside of intransitive loops.

Estimating the importance of intransitive competition in (de)stabilising species coexistence with our approach requires calculating the $\overline{\Delta r_i}$ index. It can be obtained from (1) a matrix of intra- and interspecific competition coefficients for all species pairs, (2) an empirically parameterised model able to simulate community dynamics, or (3) invasion experiments. Estimating a matrix of competition coefficients is challenging, but it can be obtained with experiments manipulating competitor density (e.g. Gremer *et al.* 2013; Narwani *et al.* 2013; Godoy *et al.* 2014) or from analyses of long-term observational data (e.g. Chu & Adler 2015). Invasion growth rates can also be estimated from empirically parameterised community assembly models (e.g. Wootton 2005) or mechanistic competition models (e.g. explicitly modelling competition for resources; Tilman 1994; Pacala & Rees 1998), even though these models may not explicitly distinguish niche partitioning and fitness differences. A potential problem for all of these approaches is that if an intransitive loop is important for coexistence, then all species in that loop need to be part of the parameterisation. As we showed, the absence of a key member greatly changes the interpretation of the dynamics, and thus the typical empirical approach of examining subsets of a community may not be appropriate. Given the efforts necessary to build such empirical models, these approaches

may not be feasible for species rich systems. An alternative empirical approach would be to directly measure invasion growth rates of focal species in the presence of the complete resident community, and then again in the absence of individual residents (following the logic of equation 5). These experimental invasions require that the resident community equilibrate before being invaded, which might only be feasible in systems with very fast generation times (such as microorganisms).

We designed the $\overline{\Delta r_i}$ index to investigate intransitive cases where pairwise species coexistence is possible, as well as cases where no stabilising difference exist and coexistence is impossible (i.e. 'pure' intransitivity; see Box 1). Assembling a pure intransitive loop in nature seems unlikely, since it requires that all species involved in the loop 'arrive' simultaneously in the community. Secondly, pure intransitivity with great fitness differences between species typically generates strong oscillations of species abundances (Vandermeer 2011), which increases the sensitivity of the system to demographic (when species are temporarily rare) and environmental stochasticity. However, as stabilising niche differences are added to a system, even if they are not strong enough to stabilise pairwise coexistence, they could slow competitive exclusion and dampen oscillations strongly enough to make the assembly of intransitive loops more likely (the substitutability of intransitivity and pairwise niche differences is shown in Appendix S6).

Overall, our analysis illustrates the various ways intransitive competition, operating against a backdrop of pairwise niche differences, can influence species coexistence. Intransitivity can stabilise or destabilise species coexistence, and many different configurations of intransitive loops can have the same stabilising or destabilising effects. Quantifying and predicting the effects of complex intransitive loop configurations on coexistence is not a simple task, but our $\overline{\Delta r_i}$ index should help make such investigations possible. A key next step in this literature, which has thus far been strongly dominated by models, will be to explore whether and how intransitive interactions contribute to the maintenance of biodiversity in natural communities.

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AUTHORSHIP

LG and PBA designed the study and JML suggested additional analyses. LG performed all analyses and wrote the first draft of the manuscript, which all authors significantly improved.

DATA ACCESSIBILITY STATEMENT

This article does not use empirical data.

REFERENCES

Allesina, S. & Levine, J.M. (2011). A competitive network theory of species diversity. *Proc. Natl Acad. Sci. USA*, 108, 5638–5642.

Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl Acad. Sci. USA*, 106, 11641–11645.

Armas, C. & Pugnaire, F.I. (2011). Plant neighbour identity matters to belowground interactions under controlled conditions. *PLoS ONE*, 6, e27791.

Buss, L.W. & Jackson, J.B.C. (1979). Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.*, 113, 223–234.

Case, T.J. (2000). *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, New York.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Chesson, P. (2012). Species competition and predation. In: *Encyclopedia of Sustainability Science and Technology* (eds Leemans, R.). Springer, New York, pp. 223–256

Chu, C. & Adler, P.B. (2015). Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecol. Monogr.*, 85, 373–392.

Diamond, J.M. (1975). Assembly of species communities. In: *Ecology and Evolution of Communities* (eds Cody, M.L., Diamond, J.M.). Harvard University Press, Cambridge, pp. 342–444.

Durrett, R. & Levin, S. (1998). Spatial aspects of interspecific competition. *Theor. Popul. Biol.*, 53, 30–43.

Gallien, L. (2017). Intransitive competition and its effects on community functional diversity. *Oikos*, 126, 615–623.

Gause, G.F. (1934). *The Struggle for Existence*. The Williams & Wilkins Co., Baltimore.

Gilpin, M.E. (1975). Limit cycles in competition communities. *Am. Nat.*, 109, 51–60.

Godoy, O., Kraft, N.J.B. & Levine, J.M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.*, 17, 836–844.

Godoy, O., Stouffer, D.B., Kraft, N.J. & Levine, J.M. (2017). Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology*, https://doi.org/10.1002/ecy.1782.

Gremer, J.R., Kimball, S., Keck, K.R., Huxman, T.E., Angert, A.L. & Venable, D.L. (2013). Wate-use efficiency and relative growth rate mediate competitive interactions in Sonoran Desert winter annual plants. *Am. J. Bot.*, 100, 2009–2015.

Huisman, J., Johansson, A.M., Folmer, E.O. & Weissing, F.J. (2001). Towards a solution of the plankton paradox: the importance of physiology and life history. *Ecol. Lett.*, 4, 408–411.

Kerr, B., Riley, M.A., Feldman, M.W. & Bohannan, B.J.M. (2002). Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature*, 418, 171–174

Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl Acad. Sci.*, 112, 797–802.

Laird, R.A. & Schamp, B.S. (2015). Competitive intransitivity, population interaction structure, and strategy coexistence. *J. Theor. Biol.*, 365, 149–158.

Lankau, R.A. & Strauss, S.Y. (2007). Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* (80-.)., 317, 1561–1563

Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.

Leyton-Brown, K. & Shoham, Y. (2008). *Essentials of Game Theory*. Morgan and Claypool Publishers.
May, R.M. & Leonard, W.J. (1975). Nonlinear aspects of competition between three species. *SIAM J. Appl. Math*., 29, 243–253.
Narwani, A., Alexandrou, M.A., Oakley, T.H., Carroll, I.T. & Cardinale, B.J. (2013). Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. *Ecol. Lett*., 16, 1373–1381.
Novak, M., Yeakel, J.D., Noble, A.E., Doak, D.F., Emmerson, M., Estes, J.A. *et al*. (2016). Characterizing Species Interactions to Understand Press Perturbations: what Is the Community Matrix? *Annu. Rev. Ecol. Evol. Syst*., 47, 409–432.
Pacala, S.W. & Rees, M. (1998). Models suggesting field experiments to test two hypotheses explaining successional diversity. *Am. Nat*., 152, 729–737.
Quinn, J.F. (1982). Competitive hierarchies in marine benthic communities. *Oecologia*, 54, 129–135.
R Development Core Team. (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.
Reichenbach, T., Mobilia, M. & Frey, E. (2007). Mobility promotes and jeopardizes biodiversity in rock-paper-scissors games. *Nature*, 448, 1046–1049.
Schreiber, S.J. & Killingback, T.P. (2013). Spatial heterogeneity promotes coexistence of rock – paper – scissors metacommunities, *Theoretical Population Biology*, 86, 1–11
Soetaert, K., Petzoldt, T. & Setzer, W. (2010). Solving differential equations in R: package de Solve. *J. Stat. Softw*., 33, 1–25.
Soliveres, S., Maestre, F.T., Ulrich, W., Manning, P., Boch, S., Bowker, M.A. *et al*. (2015). Intransitive competition is widespread in plant communities and maintains their species richness. *Ecol. Lett*., 18, 790–798.
Stevens, M.H.H. (2010). *A Primer of Ecology with R*. Use R! 2nd Editio. Springer, New York.
Tilman, D. (1982). *Resource Competition and Community Structure*. Prinecton University Press, Prinecton, New York.
Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
Ulrich, W., Soliveres, S., Kryszewski, W., Maestre, F.T. & Gotelli, N.J. (2014). Matrix models for quantifying competitive intransitivity from species abundance data. *Oikos*, 123, 1057–1070.
Vandermeer, J. (2011). Intransitive loops in ecosystem models: from stable foci to heteroclinic cycles. *Ecol. Complex*., 8, 92–97.
Wootton, J.T. (2001). Causes of species diversity differences: a comperative analysis of Markov models. *Ecol. Lett*., 4, 46–56.
Wootton, J.T. (2005). Field parameterization and experimental test of the neutral theory of biodiversity. *Nature*, 433, 309–312.

SUPPORTING INFORMATION

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